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Sexual ornaments but not weapons trade off against testes size in primates

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Abstract

Males must partition their limited reproductive investments between traits that promote access to females (sexual ornaments and weapons) and traits that enhance fertilization success, such as testes and ejaculates. Recent studies show that if the most weaponized males can monopolize access to females through contest competition, thereby reducing the risk of sperm competition, they tend to invest less in sperm production. However, how males invest in sexual ornaments relative to sperm production remains less clear. If male ornaments serve as badges of status, with high-ranking males attaining near-exclusive access to females, similar to monopolizing females through combat, their expression should also covary negatively with investment in post-mating traits. In a comparative study across primates, which exhibit considerable diversification in sexual ornamentation, male weaponry and testes size, we found relative testes size to decrease with sexual ornaments but increase with canine size. These contrasting evolutionary trajectories might be driven by differential selection, functional constraints or temporal patterns of metabolic investment between the different types of sexual traits. Importantly, however, our results indicate that the theory of relative investments between weapons and testes in the context of monopolizing females can extend to male ornaments.

Key words: Primates, ornaments, weapons, testes, trade-off, sperm competition

1. Introduction

Sexual selection is widely recognized as the evolutionary force generating divergence in male secondary sexual traits [1–3]. These traits can serve as weapons used in direct physical contests among males over access to females and/or as ornaments that signal competitive status to other males or mate quality to choosy females. Varying expression in these traits has been found to mediate male mating success [2]. However, since the females of most species throughout the animal kingdom mate with more than one male before breeding, competition among males typically continues after mating via sperm competition and cryptic female choice [4,5]. Post-mating sexual selection can favour the evolution of increased male expenditure on primary sexual traits that increase competitive fertilization success, such as testicular tissue for sperm production [6] or ejaculate features such as seminal fluid composition and sperm form and function [7,8]. Net male fitness will depend on the combined contributions of mating success and fertilization success, and therefore the differential allocation of resources between pre- and post-mating episodes of selection [9,10].

Recent theoretical treatments predict that expenditure on ejaculate production should come at a cost to male expenditure on the weapons and ornaments of pre-mating sexual selection, potentially contributing to the evolutionary divergence in secondary sexual traits found among taxa [11,12]. Males are assumed to have a limited pool of resources available for reproduction, which must be shared between pre- and post-mating sexual traits. As the strength of post-mating sexual selection increases, males are predicted to shift their allocation of resources toward ejaculate production and away from secondary sexual traits used in pre-mating competition [11]. Accumulating evidence is supporting this view. Comparative analyses have reported negative associations between testes size and male-biased sexual size dimorphism, and/or the exaggeration of weapons in taxa as diverse as parasitic worms [13], lizards and snakes [14], frogs [15], cetaceans [16] and pinnipeds [17]. Moreover, the strength of this association appears to reflect the degree to which pre-mating contest competition allows males to monopolize access to females [18]. The vast majority of this work has focused on weapons, defined strictly as physical traits used by males in direct male-male combat [19]. Few studies have examined sexual signalling traits that can serve in establishing dominance status among competing males, or in attracting females. One exception comes from work on *Alouatta* howler monkeys. Across this primate genus, those species that invest most in the development of the hyoid and larynx, allowing them to broadcast low formant-frequency vocalizations used in territorial disputes, have the smallest testes [20]. A more recent report suggests that this negative association between acoustic size exaggeration and testes size might be a more general pattern among mammals [21]. However, no studies have yet explored the evolutionary relationship between male sexual ornaments and expenditure on testes. Here, we use a

comparative analysis across primates to test whether species with exaggerated ornaments have reduced investment in their testes.

Primates are well-known for their male-biased sexual size dimorphism and the enlargement of canines used in direct male-male combat [22–24]. However, they also exhibit a range of secondary sexual ornaments that is patchily distributed across the phylogeny. Some of the best-known examples include the red chest patches of geladas (*Theropithecus gelada*), the cheek flanges of orang-utans (*Pongo* spp.), the hair capes of hamadryas baboons (*Papio hamadryas*), enlarged noses of proboscis monkeys (*Nasalis larvatus*) and the beards of men [25]. There is mounting evidence that these sexual ornaments are under pre-mating sexual selection [25]; primates typically live in social groups and these sexual ornaments play a role in the signalling of social dominance within groups, with potential consequences for male reproductive success [26–29]. For example, male orang-utans with flanged faces obtain more mating partners than do un-flanged males [30], and male proboscis monkeys with larger noses hold larger harems than those with smaller noses [31]. Male rhesus macaques (*Macaca mulatta*) with darker red facial coloration receive more solicitations from females than do males with paler faces [32], whilst men with more masculine faces are perceived as being more attractive and report a greater number of sexual partners than men with less masculine faces [33]. Primate secondary sexual ornaments thereby appear to be under sexual selection as signals [19] that indicate aggressiveness and dominance to other males to settle male–male competition over mating rights without physical conflict (badges of status), communicate male health or reproductive value to potential mates in situations of Darwinian female choice ('true' ornaments), or serve both functions [25,34]. Although empirical information is limited, male ornaments in primates are more likely to act as badges of status or play a dual function in male-male competition and female choice [25].

Primate social groups vary considerably in size and structure, and selection on ornamentation is likely to depend on the composition and size of social groups [35]. Indeed, Sheehan and Bergman [36] argued that badges of status should be absent in species that form small groups where information can be gleaned and recalled from repeated interactions with group members, but should be favoured in species that form large groups where the costs of learning and memory associated with the recognition of increasing numbers of individuals outweigh the costs of ornamentation. Consistent with this prediction, males of primate species with large group sizes exhibit more sexually dimorphic and visually conspicuous secondary sexual ornaments than those living in small groups [35]. However, an increased number of males within breeding groups is also predicted to generate increased risk and intensity of sperm competition, with evolutionary consequences for male expenditure on ejaculates [37–41]. If males face a trade-off between ornamentation and ejaculate expenditure, post-mating sexual

selection might constrain the independent evolution of ornamentation among primate species and contribute to the variation in ornamentation seen across the primate phylogeny.

Identifying a trade-off between male secondary sexual traits and testes size is notoriously difficult without considering other potentially interacting life-history, ecological and mating-system variables [12]. Ecological variables can differentially constrain the total resources available to allocate to different sexual traits, while mating-system variables can influence allocation to different traits through differences in selection acting on sexual traits. For example, in their broad taxonomic analysis, Lüpold *et al.* [18] found that negative associations between weapons and testes were only apparent among taxa in which males were able to monopolize access to females. Similarly, population density and structure were found to moderate the strength and direction of associations between male weaponry and testes size in frogs [15]. Therefore, in our analysis of the relationship between primate ornamentation and testes size we considered a suite of pre-mating secondary sexual traits, including sexual dimorphism of canines and body size, as well as social group size and the degree to which males can monopolize access to mating opportunities.

2. Material and methods

(a) Data collection and description

We compiled literature data for 103 primate species on the presence/absence of female monopolization, social group size, and sexually dimorphic traits that play important roles in male-male contest competition (sexual dimorphism in body mass and canine height [42]) and/or female choice (visual ornaments such as fleshy swellings, colourful skin patches, or hairy traits [35,43]). Sixty-four of these species also had data on combined testes mass as a post-mating sexual trait, and 42 of the latter also had data on the number of males per breeding group and the level of polygyny as alternative proxies of female monopolization [44]. The full dataset is provided in the electronic supplementary material.

We considered species to exhibit female monopolization if their social mating system is based on social groups with one dominant male and two or more females. Monogamous, polyandrous and polygynandrous mating systems were classified as non-monopolizing, and semi-solitary species (e.g., orang-utans, *Pongo* spp.) were excluded from analyses of female monopolization because the formation of social groups is a prerequisite for any long-term female monopolization to evolve. In addition to the presence/absence of female monopolization, we also estimated its importance by the number of males in breeding groups and the level of polygyny (number of adult females per male within groups). The number of males in breeding groups is inversely related to the alpha-male's paternity share (i.e., his ability to monopolize females) [37], and the relative abundance of females within groups and their reproductive

synchrony have also been linked directly to the evolution of female monopolization and associated male sexual traits [45–47].

We considered as putative sexually selected badges of status or ornaments any fleshy swellings, contrasting colouration of exposed skin areas and hairy traits such as beards, tufts, or manes. A detailed description with examples can be found in the electronic supplementary material, 'Extended description of male ornamental scoring' and table S1. Compared to most weapons, even closely related species can differ considerably in the traits that might serve as sexual ornaments, which precludes direct interspecific comparisons of the expression of homologous traits. To overcome this challenge, we focused on the degree of sexual dimorphism in non-utilitarian, ornamental structures. Previous primate studies have shown that polygynous species [43] and those that form large groups [35] exhibit much stronger male-biased expression of such traits than species with other mating systems or those with smaller groups. Although sexual dimorphism alone does not inform about total trait investment in either sex, both findings indicate a role of sexual selection in the evolution of these traits.

The only exception to estimating ornamentation based on sexual dimorphism was the genital area, which definitionally is sexually dimorphic. Yet, despite scarce information [25], it seems likely that brightly coloured genitalia (e.g., blue scrotum, red penis or perineum) that strikingly contrast with the surrounding skin or fur at least have the potential of serving as male ornaments [29]. Further, sexual dichromatism of the overall coat (e.g., many gibbon species) has not been unequivocally linked to sexual selection [48,49] and, in fact, the oftentimes less conspicuous pelage in male compared to female primates would argue against sexual selection as its main driver [48,49]. For consistency with previous studies [35,43] we retained pelage dichromatism in our scores and confirmed in a comparison with analyses excluding this parameter (electronic supplementary material, tables S2 and S3) that our conclusions are largely independent of pelage dichromatism.

Overall, we analysed sexual ornaments in two different ways. First, we updated and extended previously published metrics for ornaments, which are the sum of all potentially dimorphic traits, each of which was scored on a scale from 0 (no difference in size and colour between sexes) to 5 (males possessing a prominent visual trait that is largely or completely absent in females) [35,43].

The second approach of scoring ornamentation was similar, but more conservative. Here, we divided the body into three parts (head, trunk/limbs, and rump/anogenital area), which tend to vary independently in sexually dimorphic traits. For each body part, we scored fleshy swellings, skin patches and hairy traits. Each of these trait categories were given a value of 0 in the absence of any conspicuous sexual dimorphism, 1 for any visible sexual dimorphism in either structure or colour, or 2 for sexual dimorphism in both structure and colour. Due to the

additive nature of these traits (e.g., *Mandrillus* and some *Papio* species have many strikingly dimorphic traits in multiple body parts whereas other species differ primarily in one trait), as in the first approach we again summed across body regions all categorical scores for our analyses.

Since putative sexual ornaments are not only non-homologous between species but can also be expressed by females through social, ecological and sexual selection, including male mate choice (e.g., [50,51]), the use of sexual ornament dimorphism bears the risk of underestimating the males' total investment in display traits in any species with corresponding female expression. This can be problematic in interspecific comparisons with varying levels of female ornamentation. We therefore verified in a subset of species that males of more sexually dimorphic species also tended to be more ornamented overall than those of monomorphic species. To do so, we repeated our conservative ornamentation scoring, but this time across males within groups of closely related species that were more likely to share homologous traits but varied in their degree of sexual ornament dimorphism. In each group, we scored all pairwise species comparisons on a winner—loser—tie basis for the different structures and body parts, ranked the species by their relative level of male-specific ornamentation and compared these values with the corresponding scores of sexual ornament dimorphism (for full details, see electronic supplementary material, 'Extended description of male ornamental scoring' and figures S1–S3. All within-clade trends were positive (Spearman $\rho = 0.31–0.95$), albeit not always statically significant due to small sample sizes. Yet, combining all trends in Fisher's combined probability test indicated that, overall, male-biased sexual ornament dimorphism increases with the level of male ornamentation ($df = 16$, $\chi^2 = 50.16$, $p < 0.0001$), thus validating our use of sexual ornament dimorphism as a proxy of ornamentation in our larger-scale analyses.

Finally, we expressed the extent of sexual dimorphism in body mass and canine height as ln(male trait size / female trait size), using data from the same source for both sexes wherever possible. Further, where only volumetric testes size data were available ($n = 8$ species), we converted them to mass using the formula given in [52].

(b) Data analysis

We conducted all statistical analyses using R version 3.4.3 (R Development Core Team 2017) after log-transforming all continuous variables. To control for allometric effects, we included male body mass as a covariate in all analyses. Since the different sources, from which we extracted information on sexual size and canine dimorphism or relative testes mass, often differed slightly in the corresponding male body mass, we used the mean of all these values as our body mass covariate rather than favouring a single value that might introduce a bias to traits from other sources. However, all results were nearly identical irrespective of which body mass value was used.

Further, we accounted for phylogenetic non-independence by using phylogenetic generalized least-squares (PGLS) analyses as implemented in the R package *caper* [53], with a well-resolved molecular consensus tree for primates derived from the 10k Trees Project [54] (electronic supplementary material, figure S1). These PGLS models estimate in a maximum-likelihood approach the phylogenetic scaling parameter λ that ranges between 0 (phylogenetic independence) and 1 (complete phylogenetic dependence), thereby indicating the strength of the phylogenetic signal in the residuals [55].

Although PGLS models do not make specific assumptions about distributions of explanatory variables [56] and all our models showed a good fit, we assessed the effect of zero inflation in our scores of sexual ornament dimorphism. To this end, we repeated the above PGLS analyses while including, in addition to the ornamentation scores, a binary indicator variable separating monomorphic (ornament dimorphism value = 0) from dimorphic species (ornament dimorphism value > 0). This model tests, through the binary variable, the effect of sexual dimorphism *per se* on relative testes mass and, simultaneously in the quantitative variable, the effect of the *degree* of sexual dimorphism among the dimorphic species.

3. Results

Since none of the interaction terms were statistically significant in our analyses, we report only the simplified models based on the main effects. In a PGLS analysis including female monopolization, all premating sexual traits and body mass as explanatory variables (n = 63 species, λ = 0.61 [95%CI: 0.19–0.89]; electronic supplementary material, table S4), the combined testes were heavier in non-monopolizing than in monopolizing species (t = –4.04, p = 0.0002) and increased with sexual canine dimorphism (t = 2.49, p = 0.016). By contrast, relative testes mass decreased with the sexual ornament dimorphism (t = –3.53, p = 0.0008) whilst not being significantly correlated with sexual size dimorphism (SSD: t = 0.47, p = 0.64). The collinearity of all predictor variables was low to moderate (all variance inflation factors, VIF ≤ 3.1). When excluding the non-significant effect of SSD, the above pattern persisted (table 1), again with no indication of severe collinearity (all VIF ≤ 1.9). We also obtained nearly identical results in a model incorporating the additional indicator variable for sexual ornamentation, with no significant effect of this binary variable (t = –0.42, p = 0.67) and all previously significant effects remaining so (all $|t| \geq 2.76$, all $p \leq 0.008$, λ = 0.61 [0.20–0.89]; electronic supplementary material, table S4). Finally, the above results did not change substantively when using our more conservative ornament dimorphism scores instead of Dixson *et al.*'s [43] and Grueter *et al.*'s [35] ranking approach (all $|t| \geq 2.52$, all $p \leq 0.015$, λ = 0.66 [0.23–0.92]; electronic supplementary material, table S2), restricting the analysis to the sexually dimorphic species only (n = 30, all $|t| \geq 2.50$, all $p \leq 0.021$, λ = 0.00 [0.00–0.55]), or to those 5 clades in which our supplementary

analyses confirmed sexual ornament dimorphism to be significantly correlated with overall male-specific ornamentation (see electronic supplementary material, figure S3: $n = 21$, all $|t| \geq 2.14$, all $p \leq 0.047$, $\lambda = 0.00$ [0.00–0.74]).

As indicated in table 1 and electronic supplementary tables S3 and S5, estimating female monopolization by the number of females per male in breeding groups (and thus potential harem size) corroborated the associations between sexual traits, although the predicted effect of female bias in sex ratios itself was negative as predicted, but not statistically significant. The positive effect of increasing numbers of potentially competing males (increasingly limiting the efficacy of female monopolization) on relative testes size followed predictions of sperm competition theory (table 1 and electronic supplementary tables S3 and S5), but here the corresponding associations between sexual traits were at best weak trends (e.g., electronic supplementary table S3). Finally, using social group size as a predictor also yielded comparable results to the use of proxies of female monopolization (table 1 and electronic supplementary tables S3 and S5). Note that in all these analyses the effect of SSD or the binary indicator variable of ornamentation were not statistically significant and hence omitted, and that collinearity among predictor variables was always relatively low in all final models (all VIF ≤ 2.7).

Among the different pre-mating sexual traits themselves, none of the proxies of female monopolization had a significant effect in any PGLS model, regardless of which trait was the response variable. Therefore, and because the choice of the response variable would be arbitrary, we used a partial correlation approach based on independent contrasts rather than a PGLS model (see [57] for further justification). Due to the non-normal distribution of the ornament dimorphism scores, we employed non-parametric Kendall's rank correlations, adjusting all p-values for multiple testing using the Holm-Bonferroni method. Pairwise correlations among traits across all 102 independent contrasts (from 103 species), while holding body mass and the third sexual trait constant, revealed a positive relationship between sexual canine dimorphism and sexual ornament dimorphism (partial $\tau = 0.193$, $p_{adj} = 0.009$), although this pattern was weaker when using the more conservative ornamentation scores (partial $\tau = 0.137$, $p_{adj} = 0.043$). Irrespective of the ornamentation scoring, SSD covaried positively with canine dimorphism (partial $\tau \geq 0.207$, $p_{adj} \leq 0.007$) and tended to do so with sexual ornament dimorphism (partial $|\tau| \geq 0.118$, $p_{adj} \leq 0.083$).

4. Discussion

The evolutionary association between the *weapons* of pre-mating sexual selection and post-mating expenditure on testes size has been the subject of numerous studies (reviewed in [12]), but to the best of our knowledge only a single comparative study has examined the relationship between male expenditure on testes size and the *ornaments* of pre-mating sexual selection [20].

Here, we addressed this deficit in a comparative study of gregarious primate species and documented an evolutionary trade-off between testes mass and sexual dimorphism in pre-mating ornaments. By contrast, testes mass increased with increasing sexual dimorphism of the canines.

In addition to potential resource trade-offs, negative relationships between male weapons and testes have been explained by differential risk of sperm competition, mediated by female monopolization [11,12,18]. Specifically, if males that invest heavily in weapons are able to control access to females, they can reduce their investment in testes because female monopolization lowers the risk of sperm competition [11]. Our study of primates suggests that this explanation might extend to male sexual ornaments. Particularly if male ornaments function as badges of status, with privileged mating opportunities for highly ranked males similar to female monopolization by the most successful males in contest competition, increased investment in male ornaments should also lower the level of sperm competition and relax selection on sperm production.

The negative relationship between testes and male ornaments found across species, however, contrasts with two within-species studies of primates: Koda et al. [31] documented a positive relationship between nose size and testes volume across 18 male proboscis monkeys, whilst Setchell and Dixson [58] reported that gaining alpha rank had a positive effect on testicular size, circulating testosterone, and reddening of the facial and genital sex skin in mandrills. Within species, circulating testosterone might be the functional link between ornaments and testes. The expression of status badges such as the redness of mandrill sex skin, as well as the associated dominance, tend to be influenced by the titre of circulating testosterone [59]. Testosterone-mediated aggression is predicted particularly in unstable societies where males are repeatedly challenged by rivals over females or territories ("challenge hypothesis" [60]), with empirical evidence in at least some primates such as mandrills [58]. Since testosterone is produced by the Leydig cells within the interstitial tissue of the testes, testes size might vary in response to selection on the production of androgens in addition to, or instead of, sperm competition. For example, dominant male capybaras (*Hydrochoerus hydrochaeris*), which are characterized by large androgen-dependent scent glands involved in social hierarchy establishment, tend to have relatively larger testes, but these exhibit a greater proportion of interstitial tissue at the cost of sperm-producing tissue [61,62]. Although we are not aware of any primate study to examine such intraspecific variation in testicular morphology in relation to testosterone and sperm production, at least it seems plausible that selection on androgen production might also underlie, and functionally link, variation in testes size and male badges of status.

To what extent such a proximate explanation applies to our macroevolutionary patterns, however, remains unclear, particularly given the evolutionary trade-off between ornaments and testes found in our study. Across primates, relatively large testes are associated with higher average testosterone levels [63], but there is also anecdotal evidence that they might exhibit a relatively greater proportion of sperm-producing, and thus proportionately less interstitial, tissue [64]. The same but more robust interspecific trends are known from birds [65,66], in which the link between testosterone and male aggression was first formulated [60], before being adapted to primates (reviewed in [67]). Thus, it seems unlikely that the across-species variation in testes size would result primarily from selection on androgen production. In fact, the combined testes in our study were relatively larger in non-monopolizing than in monopolizing species and tended to decrease with increasingly female-biased sex ratios, which are congruent with predictions of sperm competition models [6] but less so with the challenge hypothesis [60]. Similarly, the increase in size-corrected testes mass with the number of males within breeding groups is indicative of higher levels of sperm competition in larger groups. Even if large groups become sub-structured (i.e. fission internally) and subunits become nucleated/insular (a phenomenon known as modularity [68,69]), sperm competition remains a risk because the spatial proximity among subunits facilitates extra-pair/extra-unit copulation (e.g. [70,71]). Thus, sperm competition does seem to be the primary agent of testes size evolution in primates as proposed previously [72].

The putative physiological link (testosterone) within some species does not necessarily transcend taxonomic levels given the dramatic diversification in sexual traits and general reproductive behaviour among primates, as well as considerable between-species variation in overall resource availability to invest in reproduction that might further complicate comparisons between taxonomic levels [12]. A possible explanation for the evolutionary trade-off between ornaments and testes mass, then, is that the increasing difficulty for males to monopolize females, reflected in the increasing testes size in response to sperm competition, might relax the benefits of investing in costly badges of status.

Unlike sexual dimorphism in ornaments, that in canine size covaried positively with testes mass. Positive relationships between weapons and testes size have been reported for other taxonomic groups [12,18], particularly those with little to no female monopolization [18]. The difference in the direction of the relationships of testes size with ornaments and weapons, respectively, is intriguing. It is too early to draw any firm conclusions, but we offer four non-mutually exclusive explanations. First, it is possible that, by signalling male status to both rival males and choosy females, male ornaments are under more intense sexual selection than canines that are involved primarily in male-male contest competition. If stronger selection results in greater trait exaggeration, ornaments might be costlier overall than the canines and

thus more likely to trade off evolutionarily against investment in sperm production, which itself can incur considerable metabolic costs [73–75]. Second, the same argument can be made if male ornaments are functionally less constrained than canines and so have the potential of becoming more exaggerated and, thus, again costlier. Third, once the permanent canines are fully expressed, even minimal metabolic investment might suffice for their maintenance. By contrast, exaggerated fleshy traits or red sexual skin, and likewise the testes, require enhanced blood supply and metabolic function throughout a male's mature lifespan. Therefore, resources allocated to reproduction have to be shared continuously between ornaments and testes, but canines are less likely to compete for the same resources as they are developed over a shorter period of time at sexual maturity. Put more broadly, a negative relationship between two traits is predicted if their total investment is fairly consistent between species but the relative allocation to each trait varies greatly, and a positive association is predicted when species vary more in their total investment than the relative allocation [12]. Fourth, it is possible that the growth of canines and testes is influenced by more closely associated genes or more similar molecular pathways than the expression of ornaments.

The positive correlation between canine dimorphism and SSD may not be surprising as both traits are widely known to increase with the degree of intra-sexual selection in primates [22,76]. However, that both traits also tended to covary positively with pre-mating ornaments in at least some analyses suggests that even weapons and ornaments do not necessarily constrain their respective evolution. One possible interpretation is again that they do not compete for the same resources and can therefore respond independently to selection (but then ornaments trade off against testes size when post-mating sexual selection is considered; see above). It could thus be argued that positive covariation between weapons and ornaments arises if male-male competition and female choice act in tandem; that is, where female choice is important, male-male competition is also important. However, this argument runs counter to Pradhan and van Schaik's [77] study showing that males do not benefit from investing in weaponry in the presence of female choice; rather, females should intrinsically disfavour weapons as they can be used for sexual coercion. An alternative explanation for the positive association between weapons and ornaments is that both are the products of male-male competition; some ornaments (e.g., badges of status) do not only constitute indicators of intrinsic viability used in female choice but also advertise fighting ability to rival males. This dual function of 'ornaments' has been established, for example, for male facial coloration in rhesus macaques [32,34] and may explain the positive covariation between badges of status and physical weapons that are used in direct combat on the rare occasion that status is challenged.

None of the proxies of female monopolization had a significant effect on any of the premating sexual traits when examined jointly. This is unsurprising given that both haremic

(with monopolization) and multimale-multifemale species (with limited monopolization) are characterized by relatively pronounced dimorphism in canine size (and body mass) [45].

In conclusion, although premating ornaments and weapons tended to covary positively with one another across primate species, the inclusion of testes size as a post-mating sexual trait unveiled an evolutionary trade-off between ornaments and testes, whilst maintaining a positive relationship with sexual weapons. These contrasting evolutionary trajectories might be driven by differential selection, functional constraints or temporal patterns of metabolic investment between the different types of sexual traits. We have previously highlighted the importance of understanding evolutionary trade-offs, or trait covariation in general, in a more comprehensive context than a simple correlation between two traits of interest [12]. Our current findings add further evidence to this notion and novel insight into the evolution of sexual traits in one of the most intensely studied mammalian taxa.

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Data accessibility

Data can be accessed from the Dryad Digital Repository (doi: 10.5061/dryad.qk514d2/1).

Authors' contributions

All authors developed the study and wrote the paper. C.C.G. and S.L. collected the data, and S.L. conducted the analyses.

Competing interests

We declare we have no competing interests.

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Table 1. Phylogenetically controlled effects of premating ornaments and weapons, and different proxies of female monopolization or social group size, on combined testes mass across primate species. Sexual ornament dimorphism was scored following Dixson *et al.* [43] and Grueter *et al.* [35]; for analyses using the more conservative approach or excluding sexual pelage dichromatism, see supplementary tables S4 and S5. All non-categorical variables except ornament dimorphism were log-transformed. Partial correlation coefficients (*r*) are listed with their lower (LCL) and upper (UCL) 95% confidence limits.

predictors	***r***	**[LCL, UCL]**	***t***	***p***
(a) presence/absence of female monopolization (N = 63, λ = 0.60 [95%CI: 0.18 – 0.88])				
body mass	0.648	[0.480, 0.754]	6.478	<0.0001
sexual ornament dimorphism	−0.420	[−0.591, −0.187]	−3.524	0.0008
sexual canine dimorphism	0.340	[0.095, 0.531]	2.758	0.008
female monopolization [yes]	−0.471	[−0.628, −0.248]	−4.061	0.0001
(b) number of males per breeding group (N = 42, λ = 0.45 [95%CI: 0.00 – 0.94])				
body mass	0.596	[0.351, 0.741]	4.518	<0.0001
sexual ornament dimorphism	−0.160	[−0.436, 0.162]	−0.983	0.332
sexual canine dimorphism	0.249	[−0.072, 0.504]	1.563	0.127
number of males	0.468	[0.179, 0.656]	3.219	0.003
(c) number of females per male in breeding groups (N = 42, λ = 0.00 [95%CI: 0.00 – 0.74])				
body mass	0.703	[0.509, 0.809]	6.015	<0.0001
sexual ornament dimorphism	−0.379	[−0.596, −0.071]	−2.490	0.018
sexual canine dimorphism	0.426	[0.128, 0.628]	2.867	0.007
polygyny level	−0.274	[−0.522, 0.046]	−1.731	0.092
(d) social group size (N = 64, λ = 0.55 [95%CI: 0.17 – 0.85])				
body mass	0.593	[0.407, 0.714]	5.652	<0.0001
sexual ornament dimorphism	−0.391	[−0.578, −0.156]	−3.267	0.002
sexual canine dimorphism	0.239	[0.014, 0.450]	1.888	0.063
group size	0.386	[0.149, 0.564]	3.212	0.002